

SCOR: Structural Classification of RNA

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SCOR Glossary -- beta version

References for motifs are the first three-dimensional structural description of the motif, and may also include reviews.

A-minor motif

This common tertiary interaction involves the insertion of minor groove edges of adenines into the minor groove of neighboring helices.

Type 0:

The N3 of the A (or other) residue is outside the O2' of the far strand of the receptor helix.

Type I:

The O2' and N3 atoms of the A residue are inside the minor groove of the receptor helix. The inserted base for the Type I interaction must be an adenine.

Type II:

The O2' of the A residue is outside the near strand O2' of the helix and the N3 of the A residue is inside the minor groove. The inserted base for the Type II interaction must be an adenine.

Type III:

The O2' and N3 of the A (or other) residue are outside the near strand O2' of the receptor helix.

References:

Nissen, P., Ippolito, J.A., Ban, N., Moore, P.B. & Steitz, T.A. 2001. RNA tertiary interactions in the large ribosomal subunit: the A-minor motif. *Proc. Natl. Acad. Sci. USA* 98:4899-4903.

adenosine platform (A platform, A-A platform)

A subset of the dinucleotide platform, the adenosine platform is formed by adjacent, coplanar adenosine bases, with hydrogen bonds forming between the N3 of the 5' A and the N6 of the 3' A.

Consensus sequence:

5' -AA- 3'

References:

Cate, J.H., Gooding A.R., Podell, E., Zhou, K., Golden, B.L., Szewczak, A.A., Kundrot, C.D., Cech, T.R. & Doudna, J.A. 1996. RNA tertiary structure mediation by adenosine platforms. *Science* 273:1696-1699.

aminoglycoside binding motif

Aminoglycosides (e.g., neomycin, kanamycin, and gentamicin) bind to the A site of 16S ribosomal RNA. Aminoglycosides also bind to other RNAs, including to the HIV-1 TAR RNA and Ribonuclease P RNA. Additionally, aptamer libraries have been designed for aminoglycoside binding. These diverse RNAs that bind to aminoglycosides are each quite different from one another in sequence and structure. Generally, aminoglycosides bind RNA in two "opened and widened deep grooves", in internal loops of non-Watson Crick double-strands.

References:

Fourmy, D., Recht, M.I., Blanchard, S.C., & Puglisi, J.P. 1996. Structure of the A Site of Escherichia coli 16S ribosomal RNA complexed with an aminoglycoside antibiotic. *Science* 274:1367-1371.

Miyaguchi, H., Narita, H., Sakamoto, K. & Yokoyama, S. 1996. An antibiotic-binding motif of an RNA fragment derived from the A-site- related region of Escherichia coli 16S rRNA. *Nucleic Acids Res* 24: 3700-3706.

Walter, F., Vicas, Q. & Westhof, E. 1999. Aminoglycoside-RNA interactions. *Curr. Opinion in Chem.*



Biol. 3:694-704.

anti-/syn- orientation about the glycosyl bond

See *syn-/anti-* orientation about the glycosyl bond.

anticodon loop

The anticodon loop is the hairpin loop on tRNA that contains the anticodon, which forms base pairs with the triplet codon sequence on mRNA. It is generally 7

bases, closed by a non-Watson Crick pair. In tRNA^{Phe}, it is closed by a A-ψ base pair. It contains a U-turn and the modified base after the anticodon.

References:

W. Saenger. 1984. *Principles of Nucleic Acid Structure*. Springer-Verlag New York Inc. New York, NY USA.

ANYA tetraloop (RNYA tetraloop)

First identified in studies of aptamers binding to the MS2 coat protein, when bound to protein, the ANYA tetraloop has two bases in the 5' stack and two looped-out bases that interact with protein. In its apo- form, the ANYA tetraloop is closed by a Watson Crick/Sugar Edge base pair, but with the first base in the 5' stack and the fourth base in the 3' stack.

Consensus sequence:

5' -ANYA- 3'

References:

Convery, M.A., Rowsell S., Stonehouse N.J., Ellington A.D., Hirao I., Murray J.B., Peabody D.S., Phillips S.E., & Stockley P.G. 1998. Crystal structure of an RNA aptamer-protein complex at 2.8 Å resolution. *Nat. Struct. Biol.* 5:133-9.

Rowsell S., Stonehouse N.J., Convery M.A., Adams C.J., Ellington A.D., Hirao I., Peabody D.S., Stockley P.G., & Phillips S.E. 1998. Crystal structures of a series of RNA aptamers complexed to the same protein target. *Nat. Struct. Biol.* 5:970-5.

base triples

Base triples are formed by three interacting, co-planar bases. These interactions are primarily non-Watson Crick. In the SCOR base triple classification, the classes are defined by the relationship between the sequence numbers of the triple residues and those of the surrounding helical stack.

Major groove triple

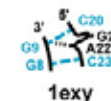
When the least-paired base in the triple, base N, is in the major groove between the adjacent base pair in the class N+1, or adjacent to the second subsequent base pair in the class N+2, or the third subsequent base in class N+3 for the major groove triples.

Minor groove triple

A minor groove triple, N-1 or N-2, is formed when the least-paired base lies in the minor groove, with either the adjacent base pair in the class N-1 or the second subsequent adjacent bases in class N-2.

References:

Klosterman, P.S., Hendrix, D.K., Tamura, M., Holbrook, S.R., & Brenner S.E. 2004. Three-dimensional motifs from the SCOR: Structural Classification of RNA database - extruded strands, base triples, tetraloops, and U-turns. *Nucl. Acids Res. Submitted*.



bulge (bulge loop)

A bulge is an internal loop consisting of one or more unpaired residues on one strand, closed on both sides by residues that are Watson Crick base paired.



child class (subclass)

A child class or subclass within SCOR has all of the attributes of its parent class. For example, "GNRA loops" is a child of "U-turn", and indeed, GNRA loops are a

form of U-turn. In the DAG structure, there may be more than one path to the child class. Additionally, SCOR follows the model from modern phylogenetics, allowing an arbitrary number of levels, or subclasses.

cis- orientation about the glycosidic bonds

See *trans*- orientation about the glycosidic bonds.

classification

A classification is an arrangement or categorization of data. SCOR is a classification of RNA structures, and contains within it a structural classification (with internal loop and hairpin loop classifications), a motif function classification and an RNA tertiary interaction classification.

class

Within SCOR, a class is a grouping of data within a classification. It may contain child classes (or subclasses). An example of a class from the structural classification within SCOR is "Loops with cross-strand stack".

coaxial helices

Nucleotide bases from two separate helices stack to form coaxial helices as a pseudo-continuous helix. Coaxial helices are highly stabilizing tertiary interactions and are seen in several large RNA structures, including tRNA, pseudoknots, the group I intron P4-P6 domain, and in the Hepatitis Delta Virus ribozyme.

cross-strand stack (cross-strand purine stack)

Cross-strand stacking occurs when a base on one strand stacks with a base on the opposing strand, rather than stacking with the adjacent bases on its own strand. It was first identified as a motif in 5S rRNA as a "cross-strand purine stack", but has subsequently been seen in other RNA structures, composed of bases other than purines. A special type of cross-strand stack is the "stack swap".

References:

Correll, C.C., Freeborn, B., Moore, P.B. & Steitz, T.A. 1997. Metals, motifs, and recognition in the crystal structure of a 5S rRNA domain. *Cell* 97:705-712.

CUUG tetraloop (CUUG tetraloop, CUNG tetraloop)

First identified in comparative sequence studies by Woese et al. (*Proc. Natl. Acad. Sci.* 87:8467-8471), solution structures of a CUUG tetraloop show it to be a diloop, with the C and G Watson Crick base paired. In ribosomal RNA structures, CUUG forms a hairpin loop with two bases in the 5' stack.

Consensus sequence:

5' -CUUG- 3'

References:

Jucker, F.M. & Pardi, A. 1995. Solution structure of the CUUG hairpin loop: a novel RNA tetraloop motif. *Biochemistry* 34: 14416-14427.

D-loop (dihydrouracil loop)

In the tRNA molecule, the D-loop contains the modified nucleotide dihydrouridine. It is composed of 7 to 11 bases and is closed by a Watson Crick base pair. The D-loop and T-loop form a tertiary interaction in tRNA.

References:

Quigley, G.J. & Rich, A. 1976. Structural domains of transfer RNA molecules. *Science* 194:796-806.
W. Saenger. 1984. *Principles of Nucleic Acid Structure*. Springer-Verlag New York Inc. New York, NY USA.

DAG (directed acyclic graph)

In a directed acyclic graph, each child node, or vertex, may have one or more

parents. The SCOR classification is represented as a DAG.

References:

Ashburner, M., Ball, C.A., Blake, J.A., Botstein, D., Butler, H., Cherry, J.M., Davis, A.P., Dolinski, K., Dwight, S.S., Eppig, J.T., et al. 2000. Gene Ontology: tool for the unification of biology. *The Gene Ontology Consortium, Nature Genet.*, 25:25-29.

dinucleotide platform

A general case of the adenosine platform, a dinucleotide platform is formed when bases of two adjacent residues are coplanar and non-Watson Crick base-paired. While originally thought to be formed of purines, the analysis within SCOR has found that there is no strong sequence pattern. Dinucleotide platforms are commonly found to be involved in base triples.

References:

Wimberly, B.T., Guymon, R., McCutcheon, J.P., White, S.W., & Ramakrishnan, V. 1999. A detailed view of a ribosomal active site: the structure of the L11-RNA complex. *Cell* 97:491-502.
Klosterman, P.S., Hendrix, D.K., Tamura, M., Holbrook, S.R., & Brenner S.E. 2004. Three-dimensional motifs from the SCOR: Structural Classification of RNA database - extruded strands, base triples, tetraloops, and U-turns. *Nucl. Acids Res. Submitted*.



double helical region

Double helical regions are continuous, linked, stacked, base-paired (but not necessarily Watson Crick base-paired) regions of RNA.

double helix (double strand, double helical stack)

RNA forms anti-parallel double helices, with the nucleotides linked together by the 3',5'-phosphodiester bonds, with the bases forming Watson Crick base pairs along the helical axis.

extended continuous stack

Extended continuous stacks are double helical regions that are bridged by base stacking, either through single base stacks or double stacks. Coaxial helices are a subset of extended double helical regions.

external stacked base

An external stacked base refers to a base that is "extruded" from a loop or helix and stacking with another base. It may form part of an extruded helical stack.

extruded helical stack (extruded helical single strand, external stacked bases)

The extruded helical strand was identified in the classification effort of SCOR 1.1. It consists of two or three unpaired bases extruded from the main double helical stack forming an independent stack. In hairpin loops it is commonly opposite a continuous helical stack in the opposing strand.

References:

Klosterman, P.S., Hendrix, D.K., Tamura, M., Holbrook, S.R., & Brenner S.E. 2004. Three-dimensional motifs from the SCOR: Structural Classification of RNA database - extruded strands, base triples, tetraloops, and U-turns. *Nucl. Acids Res. Submitted*.



GNRA tetraloop

First identified in comparative sequence studies of the ribosome, the GNRA tetraloop is very common and found in Group I intron and the Hammerhead ribozyme. First structurally characterized by NMR, the GNRA loop has a classical conformation of one base in the 5' stack, and three in the 3' stack.

Consensus sequence:

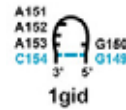
5' -GNRA- 3'

References:

Heus, H.A., & Pardi, A. 1991. Structural features that give rise to the unusual stability of RNA hairpins containing GNRA loops. *Science* 253:191-195.

hairpin loop (external loop, terminal loop, stem loop)

Hairpin loops are regions where the RNA molecule has folded back on itself and nucleotides from the molecule come together. The loop is formed of a single strand, with the characteristic "hairpin" formed by unpaired bases. The loop is closed by Watson Crick base pairs.



helical bending

Certain motifs, such as dinucleotide platforms, cause RNA A-helices to bend. The "Helical bending" class in the Internal Loops classification of SCOR includes examples of helical bend that are not caused by motifs known to cause helical bending.



hook turn

A sharp bend in a strand that is helical, A form-like, on its 5' side, with a ~180° turn in backbone direction on the 3' side that occurs between two residues, usually a sheared A-G base pair.

Consensus sequence:

5' --NUAGY--3'
3' --YRAGGR--5'

References:

Szep, S, Wang, J. & Moore, P.B. 2003. The crystal structure of a 26-nucleotide RNA containing a hook-turn. RNA. 9:44-51.

interdigitated bases (intercalated bases)

Bases within internal or hairpin loops can interdigitate, alternating stacking between bases on each strand of the loop in such a manner that the bases interlock. Interdigitated bases are seen in the D-loop:T-loop tertiary interaction in transfer RNA.

References:

Holbrook, S.R. & Kim, S.-H. 1979. Intercalation conformations in single- and double-stranded nucleic acids. Int'l. J. Biol. Macromol. 1:233-240.



internal loop (interior loop)

Internal loops are formed by an interruption of Watson Crick base pairing within a double helix. This interruption may be on one strand (sometimes called a bulge) or both strands. The helix can remain fully base paired, and also be an internal loop if non-canonical base pairs are formed by residues from both strands. An internal loop is closed on both sides by Watson Crick pairs.



junction loop (helical junction, multibranch junction, multibranch loop)

Junction loops are formed when three or more helices come together. The helices can stack coaxially in the junctions.

References:

Lilley, D.M. 2000. Structures of helical junctions in nucleic acids. Q. Rev. Biophys. 33:109-159.

kink turn (K-turn)

Formed by two strands in a helix-internal loop-helix arrangement, this turn is named for the kink that is formed in the phosphodiester backbone of the strand.

Consensus sequence:

5' --GCRNNGANG--3'
3' --CG---AGNC--5'

References:

Klein, D.J., Schmeing, T.M., Moore, P.B. & Steitz, T.A. 2001. The kink-turn: a new RNA secondary structure motif. EMBO J. 20:4214-4221.



kissing hairpin

The kissing hairpin complex is a tertiary interaction formed by base pairing between the single-stranded residues of two hairpin loops with complementary sequences.

References:

Chang, K.Y. & Tinoco I, Jr. 1994. Characterization of a "kissing" hairpin complex from the human immunodeficiency virus genome. Proc. Natl. Acad. Sci. USA 91:8705-8709.

lonepair triloop

Identified by covariation analysis of 16S ribosomal RNA sequences and in the T loop in the tRNA crystal structures, the lonepair triloop is characterized by a single base pair, either Watson Crick or non-canonical, capped by a hairpin loop containing three nucleotides. The bases immediately outside the motif (5' to the 5' end, and 3' to the 3' end) are not base-paired to one another. This motif is frequently seen in tertiary interactions.

Consensus sequences:

Type R1: 5' --UGNRA--3'

Type R2: 5' --UUYRA--3'

Type R3: 5' --NRWAN--3'

Type R4: 5' --NRYAN--3'

Type R5: 5' --NCNUN--3'

References:

Lee, J.C., Cannone, J.J. & Gutell, R.R. 2003. The lonepair triloop: A new motif in RNA structure. J. Mol. Biol. 325, 65-83.

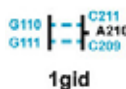
looped-in base

Looped-in bases occur within internal loops and hairpin loops. A looped-in base faces into the loop, but is not base-paired (or stacked) with other bases in the loop. See examples from "Loops with unpaired, unstacked, looped-in bases" in the Internal Loops classification.



looped-out base

A single, or several bases extend outside of a double helical stack or single stack within an internal loop or hairpin loop. The loop may be made up of Watson Crick base pairs or non-Watson Crick base pairs.



motif (structural motif)

A conserved structural pattern defined by base stacking, base pairing, backbone conformation, backbone interactions, and nucleic acid sequence. The motif is the structural module of classification for the SCOR database.

non-Watson Crick pair (non-canonical base pair)

Two bases of any type (purine-purine, purine-pyrimidine, etc.) interacting in a generally planar arrangement can form hydrogen bonds in characteristic bonding patterns. The canonical pairing of A-U and G-C with the canonical hydrogen bond patterns (see Watson Crick base pair) are Watson Crick pairings. There are stable pairings and hydrogen bond patterns that are non-Watson Crick, where hydrogen bonds form between bases on the Hoogsteen edge or sugar edge of the bases. Examples of both Watson Crick and non-Watson Crick pairings can be viewed at the [Non-Canonical Base Pair Database](#).

References:

W. Saenger. 1984. Principles of Nucleic Acid Structure. Springer-Verlag New York Inc. New York, NY USA.

Nagaswamy, N., Voss, N., Zhang, Z., & Fox, G.E. 2000. Database of non-canonical base pairs found in known RNA structures. Nucl. Acids. Res 28:375-376.

Leontis N.B., Stombaugh J., & Westhof E. 2002. The non-Watson-Crick base pairs and their associated isostericity matrices. Nucl. Acids Res. 30:3497-3531.

pseudoknot

When bases pair between nucleotides loops (hairpin or internal) and bases outside the enclosing loop, they form a pseudoknot. This structure often contains coaxial helices. It can be a very stable tertiary interaction. A database of known pseudoknots is available from [PseudoBase](#).

References:

Shen, L.X. & Tinoco, I. Jr. 1995. The structure of an RNA pseudoknot that causes efficient frameshifting in mouse mammary tumor virus. J. Mol. Biol 247:963-978.

reversed U-turn

This heptaloop was originally characterized as a region of the HDV ribozyme. Unlike another, well-characterized heptaloop, the anti-codon loop from the yeast phe-tRNA structure which contains the UNR, or U-turn, the turning phosphate in this motif is the phosphate that precedes, rather than follow, the U. It was thus named the "Reversed U-turn". The turn is stabilized by base stacking and by a hydrogen bond between the hydroxyl group of the sugar of the U and the stacking phosphate from the preceding nucleotide.

References:

Kolk, M.H., Heus, H.A. & Hilbers, C.W. 1997. The structure of the isolated, central hairpin of the HDV antigenomic ribozyme: novel structural features and similarity of the loop in the ribozyme and free in solution. EMBO J. 16:3685-3692.

ribose zipper

The ribose zipper is a tertiary interaction formed by consecutive hydrogen-bonding between the backbone ribose 2'-hydroxyls from two regions of the chain interacting in an anti-parallel manner.

References:

Cate, J.H., Gooding A.R., Podell, E., Zhou, K, Golden, B.L., Kundrot, C.D., Cech, T.R. & Doudna, J.A. 1996. Crystal structure of a Group I Ribozyme Domain: Principles of RNA Packing. Science 273:1678-1685.

Tamura, M. & Holbrook S.R. 2002. Sequence and structural conservation in RNA ribose zippers. J. Mol. Biol. 320:455-474.

S-turn (Loop E motif, bulged G motif, S-motif, bulged-G cross-strand A stack)

A common motif common to the sarcin/ricin loop and the loop E of eukaryotic 5S ribosomal RNA, the S-turn is characterized by a sheared A-G pair, a trans-Hoogsteen U-A pair, a bulged base, frequently a G, and a trans(locally parallel)-Hoogsteen-Hoogsteen A-A pair or A-C pair. This motif has been found to stabilize internal loops and junction loops in 16S and 23S ribosomal RNAs.

Consensus sequence:

5' -GA-AY-3'

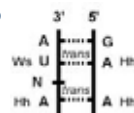
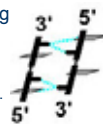
3' -AUGAY-5'

References:

Wimberly, B., Varani, G. & Tinoco, I. Jr. 1993. The conformation of loop E of eukaryotic 5S ribosomal RNA. Biochemistry 32, 1078-1087.

Szewczak, A.A., Moore, P.B., Chan, Y.-L. & Wool, I.G. 1993. The conformation of the sarcin/ricin loop from 28S ribosomal RNA. Proc. Natl. Acad. Sci. USA 90, 9581-9585.

Leontis, N.B., & Westhof, E. 1998. A common motif organizes the structure of multi-helix loops in 16S and 23S ribosomal RNAs. J. Mol. Biol. 283:571-583.



sarcin-ricin loop

The 17-base sequence of the eukaryotic sarcin-ricin loop (15 bases in prokaryotes) is one of the most highly conserved in ribosomal RNAs. Sarcin cleaves a phosphate bond, and ricin depurinates an adenine in this motif. Cleavage of this loop prevents the binding of elongation factors, and thus proper function of the ribosome. The motif is actually an assembly of three motifs: an

A-form helix, an S-turn, and a GNRA tetraloop.

Consensus sequence:

5' - CUCAGUACGAGAGGAAC - 3'

References:

Szewczak, A.A., Moore, P.B., Chan, Y.-L. & Wool, I.G. 1993. The conformation of the sarcin/ricin loop from 28S ribosomal RNA. Proc. Natl. Acad. Sci. USA 90, 9581-9585.

Szewczak, A.A., & Moore, P.B. 1995. The sarcin/ricin loop, a modular RNA. J. Mol. Biol. 247:81-98.

stack

A "stack" is a series of stacked bases, and can form a single helix. See "stacking".

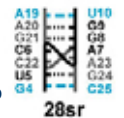
stacking (base stacking)

Nucleic acids are stabilized by base stacking, whereby bases interact through π orbitals and are stabilized by van der Waals and hydrophobic forces. Stacked bases are aligned in parallel, are approximately 3.3-3.6Å apart, and the faces of the bases overlap when viewed from the axis perpendicular to the face. A "stack" is a series of stacked bases, and can form a single helix.

References:

W. Saenger. 1984. Principles of Nucleic Acid Structure. Springer-Verlag New York Inc. New York, NY USA.

Gabb H.A., Sanghani S.R., Robert C.H., & Prevost C. 1996 Finding and visualizing nucleic acid base stacking. J Mol Graph. 14:6-11, 23-4



stack swap

Within a strand, stacking usually occurs between adjacent bases in the strand.

Stack swap occurs when a base on one strand stacks with a base on the opposing strand, resulting in a "swapping" in the stacks of the strands. Stack swap is a special case of cross-strand stacking.

strand

A covalently linked sequence of RNA residues. It has polarity from the 5' to the 3' direction.

subclass

See child class.

syn-/anti- orientation about the glycosyl bond

Relative to the glycosyl bond (the C1'-N link), a base can adopt two main orientations: *syn-* or *anti-*. Note that this terminology is a description of the orientation of the base to the sugar within a nucleoside, while the *trans-* and *cis-* terminology refers to the orientation of base pairs to the sugar-phosphate backbone.

References:

W. Saenger. 1984. Principles of Nucleic Acid Structure. Springer-Verlag New York Inc.

T-loop (TψC-loop)

First recognized in the tRNA molecule, TψC-loop (generally called the T-loop, but specifically the TψC-loop in tRNA) contains thymine, a base usually found in DNA and pseudouracil (ψ). The TψC-loop and D-loop form a tertiary interaction in tRNA. The characteristic T-loop is a 5-base strand closed by a trans-Watson Crick/Hoogsteen base-pair interaction between bases N and N+4, frequently U-A, a hydrogen bond between the imino hydrogen of the N+1 residue and the phosphate oxygen of the N+4 residue, and a hydrogen bond between the sugar hydroxyl of the N+1 residue and the N7 purine of the N+3 residue. The N+3 base is commonly an adenosine, probably conserved because it is involved in tertiary interactions.

Consensus sequence:

5' - U(G/U)NR(A/U) - 3'

References:

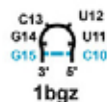
Quigley, G.J. & Rich, A. 1976. Structural domains of transfer RNA molecules. Science 194:796-806.
Nagaswamy, U. & Fox, G.E. 2002. Frequent occurrence of the T-loop RNA folding motif in ribosomal RNAs. RNA 8:1112-1119.
Krasilnikov, A.S. & Mondragon, A. 2003. On the occurrence of the T-loop RNA folding motif in large RNA molecules. RNA 9:640-643.

tetraloop motifs (see ANYA, CUYG, GNRA, (U/A)GNN, UNCG)

Several tetraloop motifs have been discovered, primarily by comparative sequence analysis. These conserved hairpin loops, capped by four bases, form turns that often mediate tertiary interactions or RNA-protein interactions.

References:

Woese, C.R., Winker, S., & Gutell R.R. 1990. Architecture of ribosomal RNA: constraints on the sequence of "tetra-loops". J. Mol. Biol. 87:8467-8471.



tetraloop receptor (GAAA tetraloop receptor)

First identified by comparative sequence analysis, this 11-nucleotide motif is conserved in Group I and Group II introns and bacterial RNase P. This tertiary interaction is characterized by a specific hydrogen bond pattern between the tetraloop and the internal loops that form the tetraloop receptor: between the first A of the tetraloop and the U-A of the receptor to form the A-U-A triple; between the second A of the tetraloop and the backbone of the receptor C and U; between the third A of the tetraloop and the C:G pair of the receptor.

Consensus sequence:

5' - CC-UAAG-3'
3' - GGUA--U-5'

References:

Pley, H.W., Flaherty, K.M. & McKay, D.B. 1994. Model for an RNA tertiary interaction from the structure of an intermolecular complex between a GAAA tetraloop and an RNA helix. Nature, 372, 111-113.
Cate, J.H., Gooding A.R., Podell, E., Zhou, K., Golden, B.L., Kundrot, C.D., Cech, T.R. & Doudna, J.A. 1996. Crystal structure of a Group I Ribozyme Domain: Principles of RNA Packing. Science 273:1678-1685.
Butcher, S.E., Dieckmann, T., & Feigon, J. 1997. Solution structure of a GAAA tetraloop receptor RNA. EMBO J. 16:7490-7499.

trans-orientation about the glycosidic bonds

The glycosidic bonds of two paired bases are oriented in *trans*- relative to a line that is parallel to and through the center (for three hydrogen bonds) or in between (for two hydrogen bonds) the base-to-base hydrogen bonds. For canonical Watson Crick base pairing, the orientation of the bases about the glycosidic bonds is *cis*-.

References:

Leontis, N. & Westhof, E. 1998. Conserved geometrical base-pairing patterns in RNA. Q. Rev. Biophys. 31:399-455.
Leontis, N. & Westhof, E. 2001. Geometric nomenclature and classification of RNA base pairs. RNA 7:499-512.



(U/A)GNN tetraloop

The (U/A)GNN tetraloops were first described as the recognition site for RNase III endoribonucleases. Structural characterization showed that the tetraloops AGAA and AGUU, both recognized by the *Saccharomyces cerevisiae* RNase III, and takes on the same fold as the UGAA tetraloop seen in the 18S rRNA of *S. cerevisiae*. This tetraloop has two bases in the 5' stack and one base in the 3' stack.

Consensus sequence:

5' - (U/A)GNN-3'

References:

Butcher, S.E., Dieckmann, T., & Feigon, J. 1997. Solution structure of the conserved 16 S-like

ribosomal RNA UGAA tetraloop. J. Mol. Biol. 268: 348-358.

Wu, H., Yang, P.K., Butcher, S.E., Kang, S., Chanfreau, G., & Feigon, J. 2001. A novel family of RNA tetraloop structure forms the recognition site for *Saccharomyces cerevisiae* RNase III. EMBO J. 20: 7240-7249.

U-turn (Π-turn)

Originally described as the uridine turn and described by the sequence U-(Any ribonucleotide)-(A or G), the U-turn is structurally characterized by a sharp bend in the direction of the phosphate-sugar backbone between the first and second nucleotides, stabilized by a hydrogen bond between the G amino proton (or U imino proton) and the phosphate group of the A (or phosphate group following the R, and a hydrogen bond between 2' hydroxyl of the G (or U) and the N7 of the R. In the case of the GNRA loop, it is additionally stabilized by the closing Watson-Crick base pair, G-C.

References:

Quigley, G.J. & Rich, A. 1976. Structural domains of transfer RNA molecules. Science 194:796-806.
Holbrook, S.R., Sussman, J.L., Warrant R.W., & Kim, S.H. 1978. Crystal structure of yeast phenylalanine transfer RNA II. Structural features and functional implications. J. Mol. Biol 123:631-660.

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UNCG tetraloop

First identified in comparative sequence studies of the ribosome, the UNCG tetraloop is common and found in mRNAs, rRNAs, tRNAs and ribozymes, as well as other functional RNAs. While the UNCG tetraloop is common, it has not been found to form tertiary interactions. The structure of the UUCG hairpin loop was first determined by NMR spectroscopy as part of an RNA dodecamer, 5'-GGAC(UUCG)GUCC-3'. When an X-ray crystal structure of the same RNA dodecamer was determined, the dodecamer formed A form helices, incorporating the non-Watson Crick G-U and U-C pairs. Structurally, the UNCG hairpin loop has as its most common conformation, the U and C bases in the 5' stack, and G base in the 3' stack, and the N base looped out.

Consensus sequence:

5' - UNCG-3'

References:

Cheong, C., Varani, G., & Tinoco I. Jr. 1991. Structure of an unusually stable RNA hairpin, 5'GGAC(UUCG)GUCC. Nature 346:680-682.
Holbrook, S.R., Cheong, C., Tinoco, I., Jr., & Kim, S.H. 1991. Crystal structure of an RNA double helix incorporating a track of non- Watson-Crick base pairs. Nature 353: 579-581.

Watson Crick base pair (canonical base pair)

Experimental data by Chargaff showed that DNA had equal molar ratios of guanine to cytosine and adenine to thymine. Watson and Crick then proposed a specific hydrogen bonding pattern between pairs of coplanar bases, A-T and G-C. For RNA, the pairing is A-U and G-C. For G-C pairs, hydrogen bonds form between a hydrogen from the N4 of C and O6 of G, the N3 of C and the N1 of G, and the O2 of C and a hydrogen from the N2 of G. For A-U pairs, hydrogen bonds form between the O4 of the U and a hydrogen from the N6 of A, and a hydrogen from the N3 of U and the N1 of A.

References:

Watson, J.D. & Crick, F.H.C. 1953. Genetical implications of the structure of deoxyribonucleic acid. Nature 171:964-967.
W. Saenger. 1984. Principles of Nucleic Acid Structure. Springer-Verlag New York Inc.

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Edited 1 April 2004

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